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S06-6 Conclusion

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1 Review

This symposium addresses several important topics. That with the highest public profile is the question of whether feathered dinosaurs existed. Both Zhong-He Zhou and Richard Prum agree that dinosaurs did indeed have feathers. My personal view is that, because in some dinosaurs we see large feather-like structures which resemble avian feathers as much as the large feathers of *Archaeopteryx*, we must conclude that these dinosaurian features are homologuous with avian feathers. A difficulty with this view is the apparently plumulaceous nature of the small body feathers in dinosaurs, which suggests that among theropod dinosaurs there were diverse integumental appendages, some of which may not be homologous with avian feathers.

Another important topic concerns the evolutionary origin of feathers. Dominique Homberger, Alan Brush and Richard Prum brought new ideas and new emphases to this issue. Homberger, in an oral, unsubmitted, advanced the new hypothesis that the evolution of feathers is linked functionally with streamlining of the body; a abstract is published in the Abstract Volume for the Congress. Brush and Prum argue that the evolution of feathers passed through stages resembling those of the developing feather. An important plank of their developmental hypothesis is the novel appearance of the follicle from which the unbranched tubular protofeather grows.

This developmental hypothesis has strengths and weaknesses. One weakness is that it does not address function. Function is such an integral part of evolutionary thinking that we need to incorporate it in any reasonably complete theory of the evolution of feathers. A strength of their hypothesis is that it integrates biochemical, genetic, developmental and morphological data. The work of Brush and Prum represents a significant contribution to the understanding of feather evolution.

2 Prospect

I wish to emphasize in these concluding remarks that there are basic questions concerning modern feathers which have not been answered today. I will give two examples. The first pertains to the fact that the most characteristic feature of modern contour feathers in birds is their high regularity. A very high number of barbules are spaced regularly along the barbs, which in themselves are spaced regularly along the rachis. In a belly feather of an Arctic Tern, approximately 31/2 cm long, the number of pennaceous barbules is about 90 thousand. Despite this striking complexity, no generally accepted theory for its functional significance exists. My second example is the frequently stated hypothesis that links feather evolution with thermal insulation, and has a flaw that is rarely pointed out. Judged from modern feathers and the fossil evidence presented by Zhou, open pennaceous feathers probably evolved before downy feathers: such feathers insulate poorly.

Other examples of unresolved issues could be given, some of them noted by Peter Stettenheim in his introduction. We need basic, thorough studies of modern feathers, along with studies of the fossil record that will deepen our understanding of modern feathers and their functioning and perhaps also their evolutionary origin.

The contributions of Homberger and Burtt exemplify the type of studies I advocate. Both provide new data and lead to the formulation of new hypotheses. Thus Homberger, in her penetrating study of the functional microanatomy of the feather-bearing integument, suggests that the depressor feather muscles, which are unique to birds, play a role in streamlining the body during flight. Burtt, in his thorough and inspiring study of the relations between feathers and feather-degrading bacilli, puts forward the idea that dark feather development may reflect a response to the greater potential for bacterial degradation in humid climates. Both these studies stress the variety of selection pressures acting on feathers. To quote Jed Burtt: “We need to think broadly and creatively about the selection pressures acting on feathers to understand their past and continuing evolution.”

Although much work remains to be done in feather science, there is no need to hurry. Feathers have existed on our planet for more than 150 million years. They have so far been studied scientifically for no more than 150 years. Let us continue the work.